FIGURE 2. Transverse section of a leaf, and surface and sectional views of a stoma. A, Diagram of the transverse section of a leaf; B and C, portions of A, enlarged, showing the cellular details; D, sectional view (across the axis) of a stoma; E, surface view of a stoma (the broken lines marked *guard cells* are drawn at a different focus). NOTE: *aper.* = apertures; *guard c.* = guard cells; *l. epi.* = lower epidermis; *pal. t.* = palisade tissue; *res. d.* = resin ducts; *spon. t.* = sponge tissue; *stom. b.* = stomatiferous band; *subs. c.* = subsidiary cells; *u. epi.* = upper epidermis; *vas. b.* = vascular bundle.

**Leaves.** Foliage leaves are persistent, spirally arranged on the branchlets but twisted at the base into two rows in one plane. Internodes are 6 to 7 mm. long (average). Each leaf consists of a lamina and a very short petiole. Laminae are coriaceous, bifacially flattened, with the adaxial

surface upward. They are linear, often strongly falcate, acute or more often acuminate at apex and slightly oblique at base, 5–7 cm. long, 0.5–1 cm. broad. Two very prominent stomatiferous bands are present on the abaxial surface and run parallel to the elevated midrib, one on each side of it (see PLATE I, a & b). Petioles are strongly decurrent on the branchlets.

Anatomically, each lamina possesses only one large, median vascular bundle with a resin canal beneath (see FIG. 2, A & B). The assimilatory tissues consist of one to two (near and at the midrib) rows of palisade cells and numerous polygonal, elongate, and dissipated spongy cells. The upper and lower epidermis are both well defined, the former with slightly more thickened cuticle layer. Stomata are arranged in longitudinal rows, their axes oriented more or less parallel to the midrib of the leaf. Each stoma (see PLATE II, b; FIG. 2, E) is encircled by 7 to 9 subsidiary cells. Strong papillae of the subsidiary cells surround the orifice of the stomatal apparatus like a wall, while the guard cells are also heavily cutinized. Sclereids are abundant, slender, branched or unbranched at one or both ends, and generally lying between the midrib and leaf-margins and perpendicular to them (see PLATE II, b).

**Staminate strobilus.** The compound staminate strobili are produced within the large winter bud which is borne on the top of the previous year's branchlets. They are short-stalked, usually four (sometimes three, rarely two or five) together, subtended by four rows of imbricate bud-scales (see PLATE I, a; FIG. 3, A). These scales are leathery, strongly keeled and more or less pointed. The true terminal bud of these branchlets is generally in the center and is further protected by small, thin scales (FIG. 3, B); it remains dormant and resumes its activity only after expansion and withering of the surrounding compound staminate strobili.

Each compound staminate strobilus is spike- or catkin-like, from which is derived the generic name *Amentotaxus* (FIG. 3, C). When fully expanded, the compound strobilus can reach a length of 2.5 to 3 cm. or more. It consists of approximately 20 to 30 globular staminate strobili somewhat decussately arranged (though not quite regular), growing along the main axis in four rows. These globular staminate strobili are clearly recognizable especially in the middle portion of the spike, since the distal ones are overcrowded and fused, and the lowermost ones are sometimes adherent to the side (secondary) branches rather than being on the main axis itself.

The staminate strobilus is globular or ovoid, 2.5 to 3 mm. in diameter in bud (see FIG. 3, D). It is composed of 9 to 12 closely compacted microsporangiophores,[1] which are peltate, with four or five (varying from

---

[1] Since the homologous structure in *Taxus* is peltate which is strongly suggestive of *Equisetum*, and since it is subtended by a bract in *Austrotaxus* (Saxton, 1934, p. 243, f. 20 & 21) and *Pseudotaxus* (Florin, 1948 a, p. 389, f. 2), microsporangiophore is perhaps preferable, as a designation, to microsporophyll; although no trace of the subtending bracts has been found at the base of the stalk in *Amentotaxus*.
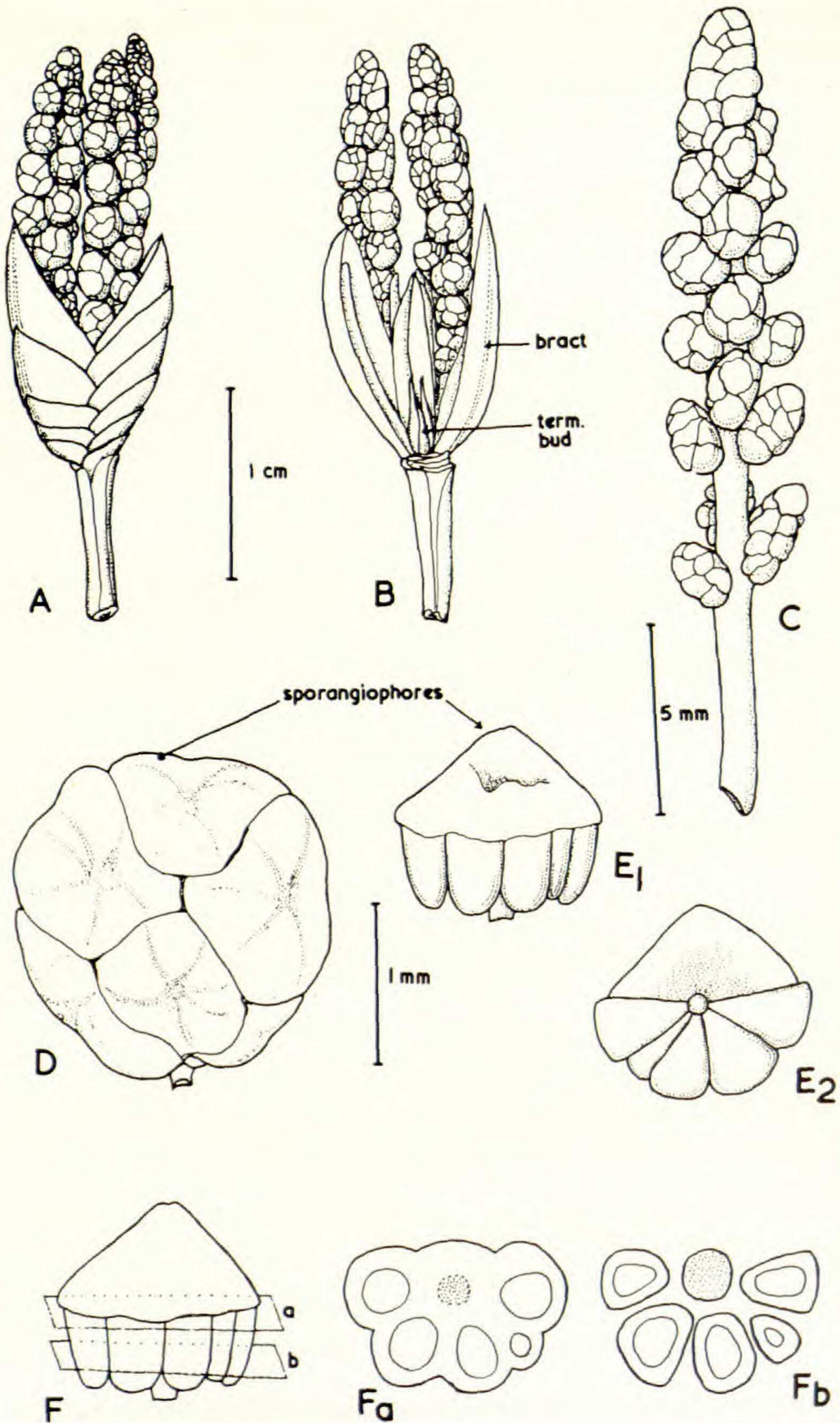
FIGURE 3. Compound staminate strobilus, staminate strobilus and micro-sporangiophore. A, External view of an unfolded winter bud, showing a cluster of four (one is not seen) compound staminate strobili; B, *the same*, with half

two to eight) microsporangia hanging underneath in a semicircle and with a short stalk near the center (see PLATE II, e; FIG. 3, E). The outline of the peltate microsporangiophores, as seen from the outer surface, varies from round to deltoid, to more commonly polygonal, due to mutual compression.

At maturity the thickened outermost layer and one or two (in part) inner layers of the microsporangial walls are retained (see PLATE II, d & e). The microspores are wingless.

**Ovulate strobilus.** The ovulate strobilus is globular to ovoid, flattened dorsiventrally (see PLATE I, b; FIG. 4, $A_1$, $A_2$, $B_1$, $B_2$, $C_1$, $C_2$). These strobili are situated singly in the axils of foliage leaves. The ovule is solitary, terminal on the strobilate axis, and subtended below by five (or six) pairs of opposite and decussate, sterile bracts; three pairs of which are lateral and prominently keeled, and the other two (or three) pairs are dorsiventral and only slightly curved (FIG. 4, $A_4$). The stalk of the strobilus is slender, about 1–1.5 cm. long, more or less flattened and narrowly winged.

Young ovules, at the stage of about 3 mm. in length (excluding the sterile bracts) (FIG. 4, $A_3$), possess an elongate conical nucellus, of which the upper part is loosely enveloped by a single layer of integument, the lower half, however, is seemingly associated only with the cupular arillus primordium. The integument (if it is interpreted as confined to the portion above the arillus only) and the arillus, at this stage, appear to be completely separated. The vascular supply to the ovule, as seen in cross section, consists of 8 to 10 normally oriented vascular bundles. They terminate at the end of the ovule far below the nucellus — neither the integument nor the arillus primordium is visibly vascularized.

In the slightly older ovules at the stage of about 5 mm. in length (FIG. 4, $B_3$), as a result of the enlargement of both the nucellus and the integument, these two parts become approximate. Also, owing to the intercalary growth of the lower half of the ovule, the integument becomes evidently embedded in the cupular arillus. The vascular supply can be observed near the base of the ovule.

In the still older ovules, at the stage of about 6.5 cm. in length (FIG. 4, $C_3$; FIG. 5), the nucellus is enveloped by and fused with the integument except for the uppermost part which remains free. Nearly two-thirds of the integument, in turn, is embedded in and completely united with the arillus. Isolated tracheids may be found in the lower part of the ovule at a fairly high level in the region where the fusion of aril and integument occurs.

of the bracts and compound staminate strobili removed, showing the hidden terminal bud inside; C, a compound staminate strobilus, showing a number of ovoid to globular staminate strobili more or less decussately arranged on an axis; D, a globular staminate strobilus (taken from the median of C), enlarged; $E_1$ and $E_2$, two views of a sporangiophore showing five microsporangia arranged in a semicircle below; $F_a$ and $F_b$, two diagrammatic sectional views of the sporangiophore.

A general outline of the tissues in the largest ovule available is shown in FIGURE 5. The arillus consists of 10 to 15 layers of parenchyma cells with rows of resinous cells lining the epidermis near the rim. The cuticle is thin. The lower portion of the integument is composed of 12 to 20 layers of small, partly closely packed, and partly loosely dissipated parenchyma cells. There is no clear distinction of the arillus from the integument below the level of fusion. The upper portion of the integument is heavily cuticularized. The cells near the micropyle are enlarged, sclerenchymatous, and oriented horizontally. The nucellus is prominently beaked; the beak is hemispheric, and composed of numerous small polygonal cells with moderately heavy walls rather loosely arranged especially towards the micropylar end. A large portion of the nucellus at this stage, is digested and replaced by the multicellular megagametophyte. Isolated tracheids and short rows of tracheids are observed at the lower part of the peripheral region where the integument and arillus are merged.

The ovular structure of *Amentotaxus* in general, as noted by several authors (e.g. Florin and others), is rather similar to that of *Torreya*; but its vasculature is very much simpler. In *Amentotaxus*, although there are 8 to 10 vascular strands entering the base of the ovule, only the isolated tracheids are present in the lower part of the ovule, in the region where the integument and arillus meet. In *Torreya*, however, there are two vascular strands running up inside the arillus nearly to the apex of the seed, each of which then sends a branch through a foramen in the stony layer of the integument; each branch forks, forming a loop which encircles the seed. Oliver (1903) proposed the "hyposperm theory" to explain this peculiar vascular structure. According to this theory, all the basal part (the "hyposperm") of the ovule is an intercalated growth and phylogenetically younger than the extreme tip (the "archisperm"). The branching of the integumental vascular bundles inwardly is also reported in *Austrotaxus* (Saxton, 1934, p. 419, *fig. 18*) and *Cephalotaxus* (Singh, 1961, p. 160, *fig. k*). In the case of *Amentotaxus*, no traces of such branching are present. With the intercalary growth of the lower part of the integument and arillus concomitantly with the enlargement of the nucellus, the integument becomes evidently embedded in the arillus and fused with it. There seems to be no evidence to prove that the lower part of the *Amentotaxus* ovule is a "hyposperm," or is phylogenetically younger than the upper part.

**Seed and seedling.** The seed is ellipsoid-oblong, drupe-like (PLATE I, c), 3.2 to 3.6 cm. long, 1 to 1.2 cm. broad, and slightly flattened dorsiventrally. The outer part of the seed coat is completely covered and fused with the arillus, except the extreme tip which is exposed (FIG. 6, A & B). The merged structure is soft-leathery in texture although the outer portion is easily blistered and disintegrated when soaked in water. The nucellus is almost entirely replaced by the ivory female gametophyte ("endosperm") which has an entire rather than ruminate margin (as in *Torreya*). The embryo is linear, lying in the center of the gametophyte.
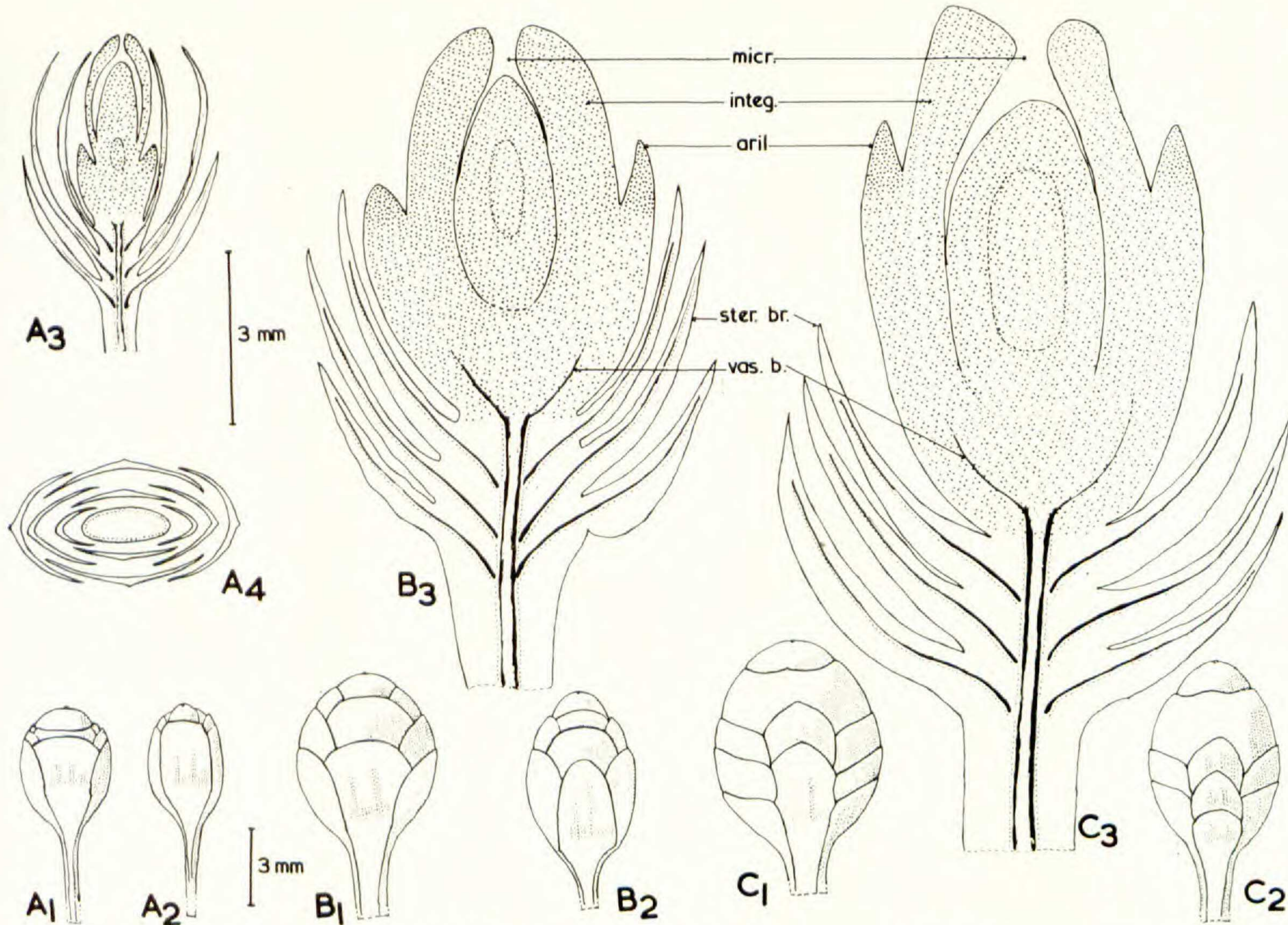
FIGURE 4. External and sectional views of three ovulate strobili. $A_1$ and $A_2$, two views of a young strobilus; $A_3$ and $A_4$, longitudinal and transverse sections of the same strobilus; $B_1$ and $B_2$, two views of a slightly older strobilus; $B_3$, longitudinal section of *the same*; $C_1$ and $C_2$, two views of an older strobilus; $C_3$, longitudinal section of *the same*; NOTE: *micr.* = micropyle; *integ.* = integument; *ster. br.* = sterile bract; *vas. b.* = vascular bundle.

In common with other conifers, germination is of epigeal type. In the one year old seedling examined (PLATE I, d), the cotyledons have dropped, but the two cotyledonary scars are clearly evident. The juvenile leaves are 3.5 to 4 cm. long, 3.5 to 4 mm. wide, with two glaucous stomatiferous bands underneath. Fundamentally of spiral arrangement, since the internodes are of variable length, the juvenile leaves appear subopposite or rarely subverticillate.

## TAXONOMIC POSITION OF AMENTOTAXUS
## AND THE CLASSIFICATION OF THE CONIFERALES

Pilger (1926) assigns *Amentotaxus*, together with *Cephalotaxus*, to the Cephalotaxaceae on the basis of the compound nature of their staminate strobili. Kudo (1931), after seeing the ovulate strobilus, hitherto unknown, maintains that "it (*Amentotaxus*) must be included in a new family Amentotaxaceae, or in a new subfamily or tribe of Taxaceae, but not in Cephalotaxaceae" (p. 311). As a result, a new family Amentotaxaceae was proposed by Kudo and Yamamoto (in Kudo, 1931). Koidzumi (1932) strongly felt that the new family was not necessary. He, therefore, established a subfamily Amentotaxoideae (including both *Amentotaxus* and *Austrotaxus*) within the Taxaceae. Later on, following his enumeration of various similarities and dissimilarities among the Taxaceae, Cephalotaxaceae, and *Amentotaxus*, he (1942), recognized that *Amentotaxus* and *Cephalotaxus* are in fact related, and moreover, suggested that Taxaceae and Cephalotaxaceae should be merged into one family and both reduced to subfamilial status. Florin (1948, 1951) emphasized the differences of ovulate strobili and stomatal structures between *Cephalotaxus* and *Amentotaxus*, and thus sustained the transference of *Amentotaxus* from Cephalotaxaceae to Taxaceae. Chuang and Hu (1965) report the chromosome number of *Amentotaxus argotaenia* (Hance) Pilger (or *A. formosana* Li) to be $x = 7$, which is different from those reported from *Taxus* ($x = 12$), *Torreya* ($x = 11$), and *Cephalotaxus* ($x = 12$). They, therefore, support Kudo and Yamamoto in maintaining *Amentotaxus* in a separate family, the Amentotaxaceae. The present writer is inclined to think that (1) *Amentotaxus* is probably better placed in the Taxaceae than in the Cephalotaxaceae or in a separate family; (2) the Taxaceae are not isolated, but are likely allied to the Cephalotaxaceae, probably through *Amentotaxus*. These two points are elaborated in the following paragraphs.

Features which distinguish *Amentotaxus* from other members of the Taxaceae such as the spicate compound staminate strobili, the peculiar stomatal structure (with larger number of subsidiary cells, thickened papillae, etc.), etc., appear to be insufficient to warrant a separate family status. The difference in chromosome number is probably inadequate to be cited as a justification for the establishment of the Amentotaxaceae.[2]

[2] For example, in a recent report (Hair & Beuzenberg, 1958) on the chromosome numbers of the Podocarpaceae, the following two closely related genera possess such
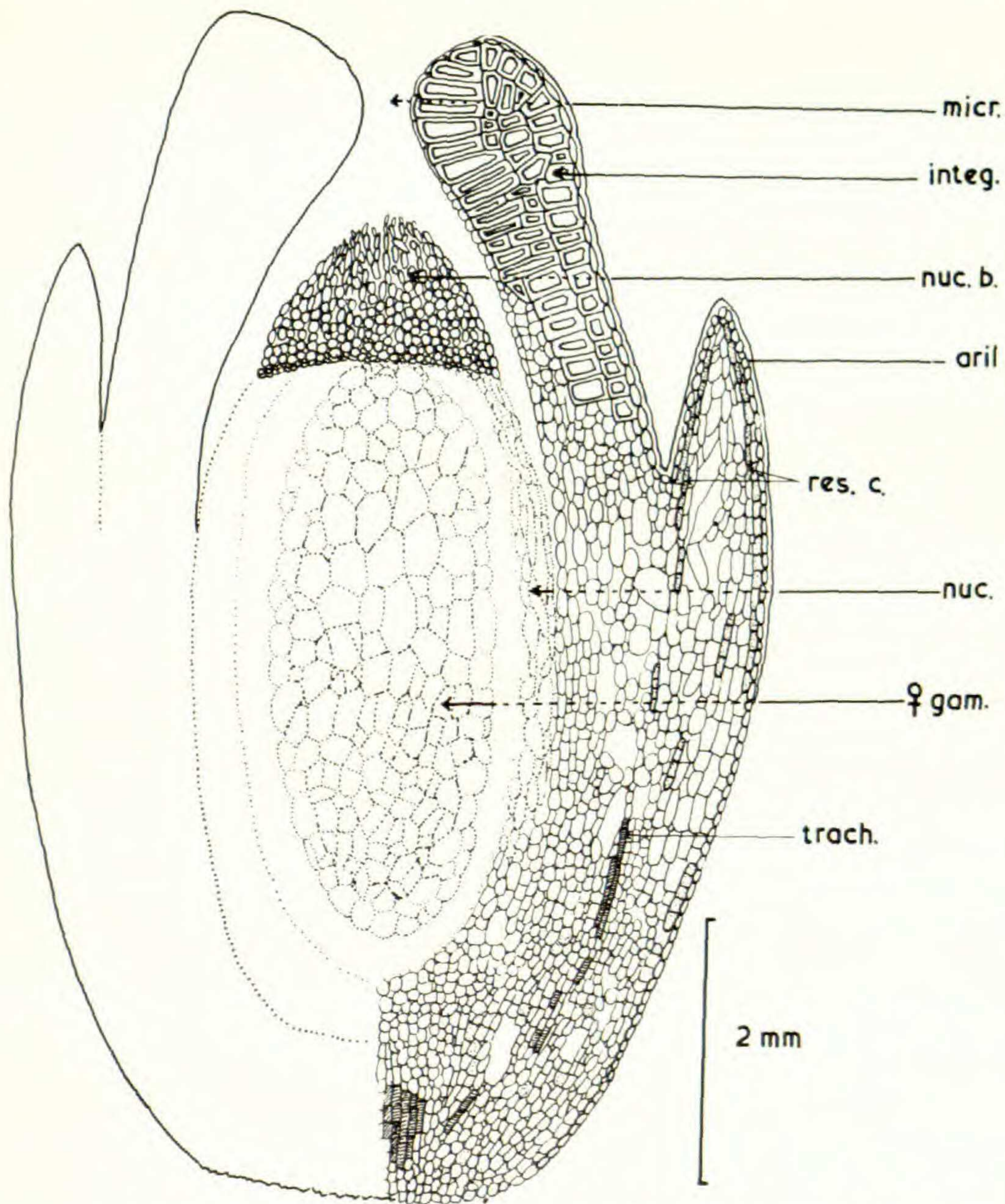
FIGURE 5. Longitudinal section of an ovule, details of Figure 4C₃. NOTE:
*nuc. b.* = nucellus beak; *res. c.* = resin cells; *nuc.* = nucellus; ♀ *gam.* =
megagametophyte; *trach.* = tracheids.

On the other hand, the resemblance of *Amentotaxus* to the Taxaceae, es-
pecially to the genus *Torreya*, in the general structure of staminate strobili,
ovulate strobili, microsporangiophores, ovules, etc. is overwhelming. There-
fore, Janchen's (1949) treatment including both *Amentotaxus* and *Torreya*
in the Tribe Torreyeae under the Taxaceae appears to be a logical one.

a range of variation: *Dacrydium* ($x$ = 15, 12, 11, 10, 9), *Podocarpus* ($x$ = 19, 18,
17, 13, 12, 11, 10); whereas other members of the family also have various different
basic numbers: *Acmopyle* ($x$ = 10), *Microcachrys* ($x$ = 15), *Pherosphaera* ($x$ = 13),
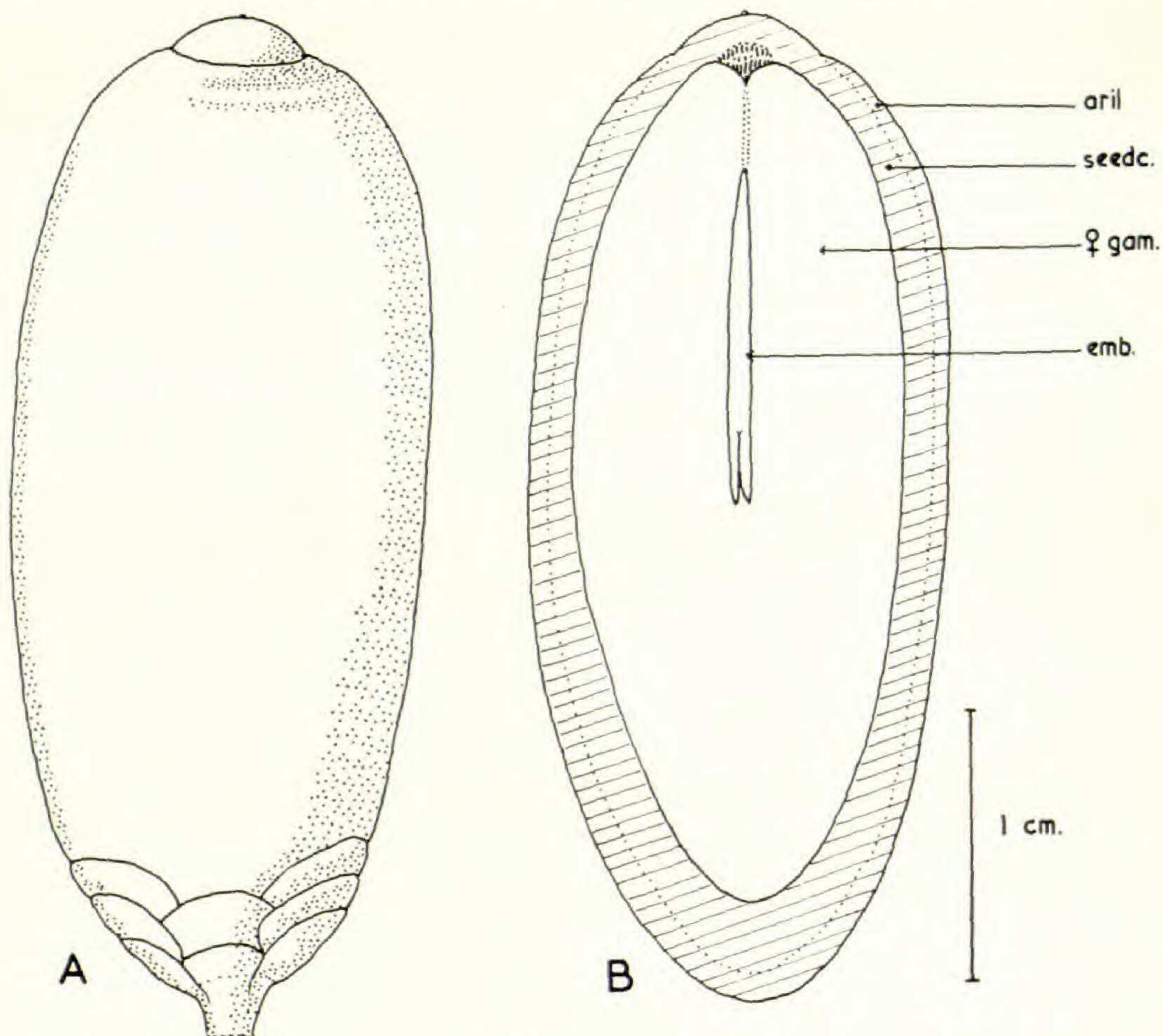*Phyllocladus* ($x$ = 9), and *Saxagothaea* ($x$ = 12).

FIGURE 6. External and sectional views of a seed.

A more or less similar view is held by Kudo (1931), Koidzumi (1932), Li (1952), and others.

Florin in a series of papers (1948, 1951, 1954) strongly advocated separation of Taxaceae (which includes the following five genera: *Taxus, Amentotaxus, Torreya, Austrotaxus,* and *Pseudotaxus* [ = *Nothotaxus*]) from the rest of the Coniferales to form a separate order, the Taxales, a view originally expressed by Sahni (1920) but modified by Florin with the exclusion of *Cephalotaxus*. A quite different scheme proposed by Buchholz (1934), was summarized by Chamberlain (1935, pp. 229, 230) as follows: The order Coniferales can be divided into two suborders: one the Pinineae (as Phanerostrobilares or Pinares) with an obvious cone, includes the Pinaceae, Taxodiaceae, Cupressaceae and Araucariaceae; the other, Taxineae (as Aphanostrobilares or Taxares) without such an obvious cone, contains the Podocarpaceae, Taxaceae, and Cephalotaxaceae.

Florin (1951, pp. 363, 364) fully endorsed Wilde's (1944) postulation that in *Podocarpus,* the species with 1-ovulate strobili are independently derived from those with multiovulate strobili, and represent the ultimate stage of reduction. In addition, his own interpretation (1951, 1954) of the ovulate strobilate structures of the modern conifers as possibly evolved from a much more complicated structure of fossil groups such

as found in the palaeozoic *Lebachia, Ernestiodendron, Walchia,* and *Pseudovoltzia,* has been widely appreciated. Paradoxically, he insists that the 1-ovulate strobilus of the Taxaceae is a primitive rather than a derived condition; therefore the family Taxaceae is of entirely different origin from the rest of the other Conifers. This is mainly because of his emphasis on the finding of 1-ovulate *Palaeotaxus* in the Triassic and *Taxus jurassica* in the Jurassic rocks. "Because of its high geological age" he noted (1951, p. 349), "*Palaeotaxus* can hardly derive from any cone-bearing type." It seems he does not realize the possible existence of the exceptionally fast rate of evolution, designated by Simpson (1944) as tachytelic evolution. Many authors, such as Chamberlain (1935, p. 439), Pulle (1937), Takhtajan (1953, p. 34), etc. express their notions that the single ovulate strobilus of taxads is most likely derived from the multi-ovulate cones. The present writer (Keng, 1963) also points out that the evolution of the ovulate strobili in the genus *Phyllocladus* (belonging to the Podocarpaceae, or according to some authors, the monogeneric family, Phyllocladaceae) might indicate the possible mode of how the single, pseudo-terminate ovule of taxads could have been achieved. Incidentally, *Phyllocladus* is somewhat intermediate between the Taxaceae and Podocarpaceae; on morphological ground it is probably correct for it to be placed in the Podocarpaceae (Maheshwari, 1962).

Although, as discussed above, *Amentotaxus* should be better classified in the Taxaceae rather than Cephalotaxaceae, it does not mean that the Taxaceae and Cephalotaxaceae are totally unrelated as suggested by Florin. The present writer agrees with Saxton (1934), Pulle (1937), Koidzumi (1942), and many others that these two families are in fact related. In this connection, it is rather interesting to mention the views of Singh (1961) who has contributed an excellent account on the life history of *Cephalotaxus drupacea* Sieb. & Zucc. In his discussion of the relationships of the Cephalotaxaceae and Taxaceae, he pointed out a number of similarities between these two families and noted that they "resemble each other in wood structure, pollen structure, and to some extent embryogeny" (p. 193). He was, unfortunately, dominated by Florin's misconception that the Taxaceae are isolated and reached the contradictory conclusion that "it appears best to regard the Taxaceae and the Cephalotaxaceae as unrelated" (p. 193).

If we accept the general view that the compound staminate strobilus is a primitive condition (Wilde, 1944), that the peltate sporangiophore is more antiquated than the dorsiventral ones (Florin, 1948), and that the one-ovulate strobilus is derived from a multiovulate strobilus (Pulle, 1937), and also if we assume that the Taxaceae and Cephalotaxaceae are phylogenetically affiliated, then an ideal ancestral form of *Taxus-Amentotaxus-Cephalotaxus* complex would hypothetically possess the following synthetic strobilate features.

Staminate or microsporangiate strobili — a cluster of spike-like compound strobili surrounding a terminal bud and enveloped by numerous bud-scales (cf. *Amentotaxus*); each compound strobilus composed of

many ovoid or globular strobili; each strobilus consisting of many peltate, spirally arranged sporangiophores with a number of sporangia on the undersurface around the stalk (cf. *Taxus, Pseudotaxus*); each peltate sporangiophore further subtended by a leafy bract (cf. *Pseudotaxus*, see Florin, 1948a, p. 389, *fig. 2*; or *Austrotaxus*, see Saxton, 1934, p. 423, *figs. 20 & 21*).

Ovulate or megasporangiate strobili — a strobilus composed of many imbricate ovuliferous scales each with several to two (or one) ovules on its upper surface (cf. *Cephalotaxus*); ovules erect, with only one integument and surrounded by a cupular arillus but free from it (cf. *Taxus, Pseudotaxus*); the integument supplied by a number of lengthwise vascular bundles, each of which gives a horizontal branch in the middle of the integument, toward the inner part of the ovule to supply the nucellus and gametophyte (cf. *Torreya*, see Oliver, 1903; *Austrotaxus*, see Saxton, 1934, p. 419, *fig. 18*; *Cephalotaxus*, see Singh, 1961, p. 160, *fig. k*).

To summarize, firstly, since the resemblance of *Amentotaxus* to *Torreya* (Taxaceae) is so overwhelming, it seems logical to include *Amentotaxus* in the Taxaceae; secondly, since the family Taxaceae is intricately affiliated to the Cephalotaxaceae on the one hand and possibly to the Podocarpaceae on the other, Buchholz's scheme of classification of the Coniferales, therefore, appears to be sound.

## ACKNOWLEDGMENTS

## LITERATURE CITED

BUCHHOLZ, J. T. The classification of Coniferales. Trans. Illinois Acad. Sci. **25:** 112, 113. 1934.

CHAMBERLAIN, C. J. Gymnosperms, structure and evolution. xi + 484 pp., *figs*. Univ. of Chicago Press. 1935.

CHUANG, T. I., & W. W. L. HU. Study of *Amentotaxus argotaenia* (Hance) Pilger. Bot. Bull. Acad. Sinica. II. (Taipeh) **4:** 10–14. 1963.

ERDTMAN, G. Pollen and spore morphology/plant taxonomy. 147 pp., *frontis.*, *5 pls*. Almqvist & Wiksell, Stockholm. 1957.

FLORIN, R. Untersuchungen zur Stammesgeschichte der Coniferales und Cordaitales, I. Sv. Vet-akad. Handl. III. **10:** 1–588. *58 pls*. 1931.

———. Die Koniferen des Oberkarbons und des unteren Perms. I–VIII. Palaeontographica **85B:** 1–729. 1938–45. [Cited in Florin, 1951.]

————. On the morphology and relationships of the Taxaceae. Bot. Gaz. **110**: 31–39. 1948.

————. On *Nothotaxus*, a new genus of the Taxaceae from eastern China. Acta Horti Berg. **14**: 385–395. 1948a.

————. Evolution in *Cordaites* and conifers. *Ibid.* **15**: 285–388. 1951.

————. The female reproductive organs of conifers and taxads. Biol. Rev. **29**: 367–389. 1954.

HAIR, J. B., & E. J. BEUZENBERG. Chromosomal evolution in the Podocarpaceae. Nature **181**: 1584–1586. (June) 1958.

JANCHEN, E. Das System der Konifern. Akad. Wien. Sitz-ber. **158**: 155–262. 1949. [Cited in Li, 1952.]

KENG, H. Taxonomic position of *Phyllocladus* and the classification of Conifers. Gard. Bull. Singapore **20**: 127–130. 1963.

KOIDZUMI, G. Notes on Amentotaxaceae. [In Japanese.] Acta Phytotax. Geobot. **1**: 185. 1932.

————. Further notes on Amentotaxaceae Kudo. [In Japanese.] *Ibid.* **11**: 135, 136. 1942.

KUDO, Y., & Y. YAMAMOTO. Amentotaxaceae. IN: KUDO, Mater. Fl. Formosa IV. Jour. Soc. Trop. Agric. (Taihoku) **3**: 110, 111. 1931.

LI, H. L. The genus *Amentotaxus*. Jour. Arnold Arb. **33**: 192–198. 1952.

MAHESHWARI, P. The overpowering role of morphology in taxonomy. Bull. Bot. Surv. India **4**: 85–94. 1962.

OLIVER, F. W. The ovules of the older gymnosperms. Ann. Bot. **17**: 451–476. 1903.

PILGER, R. Cephalotaxaceae. IN: ENGLER & PRANTL, Nat. Pflanzenfam. ed. 2. **13**: 267–271. 1926.

PULLE, A. Remarks on the system of the Spermatophytes. Med. Bot. Mus. Utrecht **43**: 1–17. 1937.

SAHNI, B. On certain archaic features in the seed of *Taxus baccata*, with remarks on the antiquity of the Taxineae. Ann. Bot. **34**: 117–133. 1920.

SAXTON, W. T. Notes on Conifers VIII. The morphology of *Austrotaxus spicata* Compton. Ann. Bot. **48**: 412–427. 1934.

SIMPSON, G. G. Tempo and mode in evolution. Columbia Univ. Press. New York. 1944.

SINGH, H. The life history and systematic position of *Cephalotaxus drupacea* Sieb. et Zucc. Phytomorphology **11**: 153–197. 1961.

SPORNE, K. R. The morphology of gymnosperms. Hutchinson Univ. Library. London. 1965.

SUGIHARA, Y. Notes on *Amentotaxus*. [In Japanese.] Bot. Mag. Tokyo **57**: 404, 405. 1943.

TAKHTAJAN, A. L. Phylogenetic principles of the system of higher plants. Bot. Rev. **19**: 1–45. 1953.

WILDE, M. H. A new interpretation of coniferous cones. I. Podocarpaceae (*Podocarpus*). Ann. Bot. II. **8**: 1–41. 1944.

YAMAMOTO, Y. Cephalotaxaceae. Suppl. Icon. Pl. Formos. **3**: 1–5. 1927.

————. Amentotaxaceae. *Ibid.* **5**: 7–11. 1932.

DEPARTMENT OF BOTANY
UNIVERSITY OF SINGAPORE
BUKIT TIMAH ROAD
SINGAPORE, 10

## EXPLANATION OF PLATES

### PLATE I

(Scale in each figure in 1 mm. divisions.)

*Amentotaxus formosana* Li. a, Cluster of compound staminate strobili from an unfolded winter bud borne on the tip of a branchlet (cf. FIG. 3A); b, solitary ovulate strobilus borne in the axil of a leaf (which has dropped off) (cf. FIG. 4, $C_2$); c, one fully mature and three young seeds (cf. FIG. 6A); d, seedling, of which the two cotyledons (on the first node) have dropped off.

### PLATE II

(Scales: in a, 150 $\mu$; in b and c, 50 $\mu$; in d and e, 200 $\mu$; in f, 2 mm.)

*Amentotaxus formosana.* a, Transverse section of a leaf showing the midrib region (cf. FIG. 2B); b, lower (abaxial) surface of a leaf (after clearing) showing the stomata and sclereids; c, stomata in transverse section (cf. FIG. 2D); d, transverse section of a microsporangiophore (cf. FIG. 3, $F_a$); e, longitudinal section of a microsporangiophore; f, longitudinal section of an ovulate strobilus (cf. FIG. 4, $C_3$).

Plate I
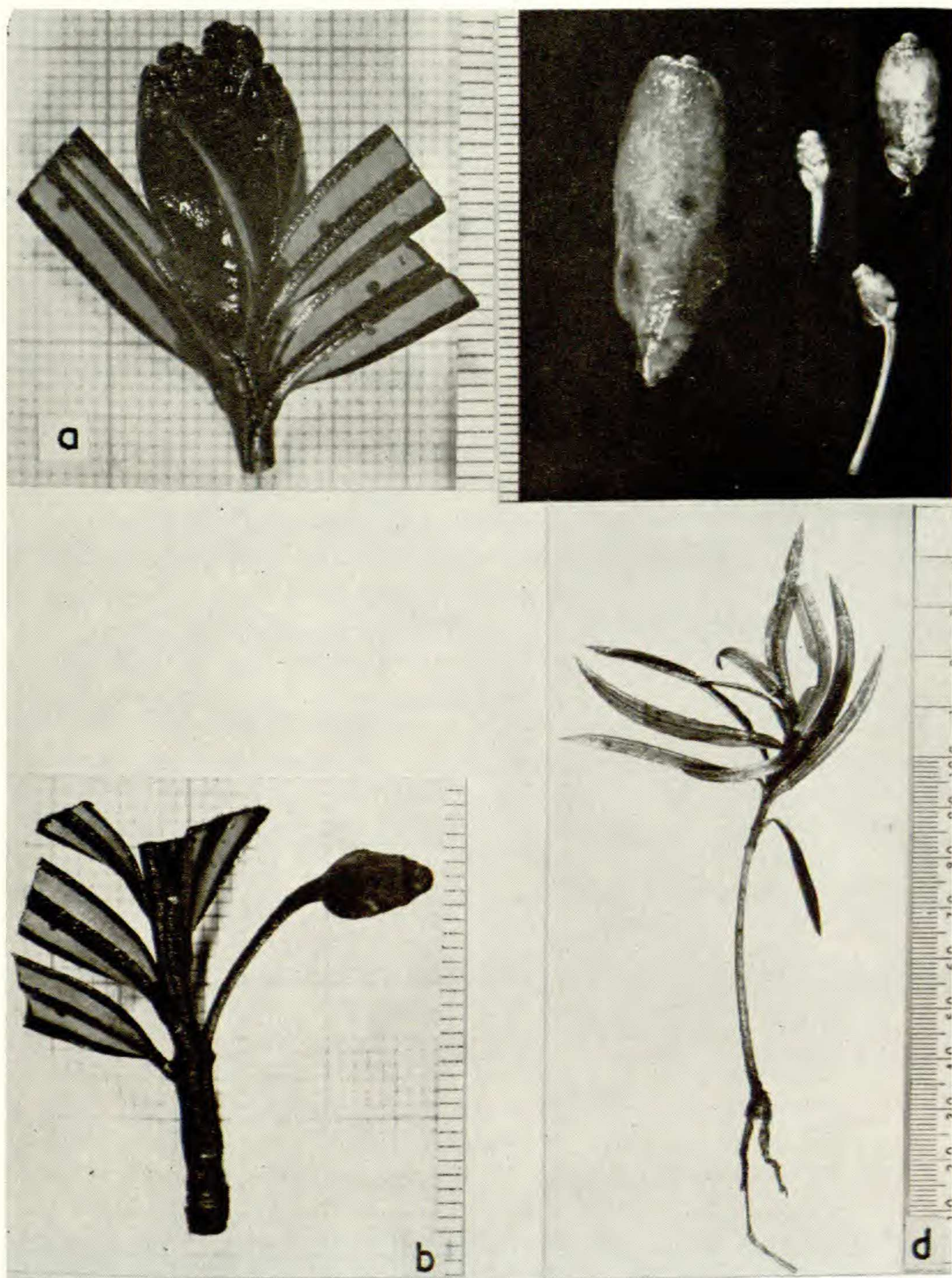


Keng, Amentotaxus formosana
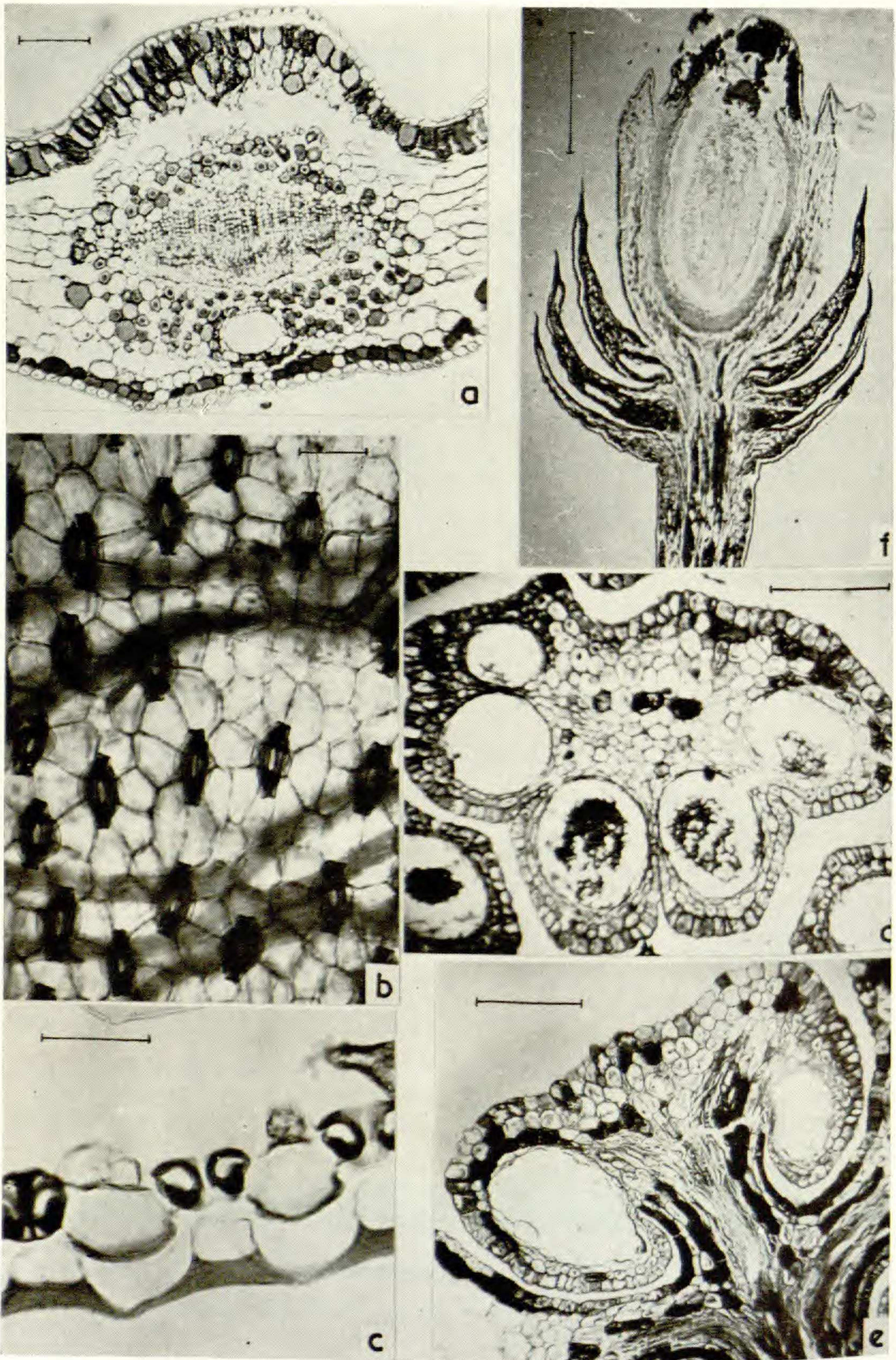
KENG, AMENTOTAXUS FORMOSANA

# A KARYOLOGICAL SURVEY OF LONICERA, II

LILY RÜDENBERG AND PETER S. GREEN *

IN THE FIRST PAPER presenting the results of this survey, all the chromosome numbers recorded for the genus *Lonicera*, to that date, were assembled, together with many new counts. Since that time the study of *Lonicera* has continued, but to bring the investigation to a conclusion all the additional counts that have been made using the Arnold Arboretum collections are presented below (together with three further records that have appeared in the literature).

Cytological methods, documentation and nomenclature used here follow those of the first paper, to which reference should be made.[1]

An attempt was made to note differences in karyotype morphology and, certainly, differences in the overall size of chromosome complements were observed between different species. Also, variation in individual chromosomes, their size, centromere position, and the presence and size of satellites were noted, but considering the relatively large number of species in the genus and the few individuals investigated, it has not proved possible to compare and correlate these differences, and their groupings, with the infrageneric classification proposed by Rehder (1903).

At metaphase the chromosomes, in many cases, were so contracted that two satellites were not always visible. Thus, it was not possible to determine whether or not *Lonicera modesta* had a satellited chromosome pair. More details of morphology could be observed at late prophase. In some cells, pretreatment with oxyquinoline (Tjio & Levan, 1950) caused a structural differentiation of the chromosomes by revealing positively and negatively heteropycnotic segments. Homologues of similar size could then be identified by the location of the centromere and by the individual distribution of these segments. A comparable pattern has been observed in several homologues of different species of *Lonicera*. FIGURES 1 to 10 present examples which were encountered of nuclei in mitosis (most examples taken from species in different subsections of Rehder's classification).

A few comments may be made. In four cases both diploid and tetraploid plants have been recorded within the same species. In *Lonicera ferdinandii* Franch., the earlier undocumented counts and all the plants at the Arnold Arboretum appear to be diploid, except for one (AA 21595) which is tetraploid. This particular bush is an old one, raised from seed of *Rock 13519* collected in S.W. Kansu, China, in 1925, yet phenotypical-

---

\* In this survey, the cytological investigations have been carried out by one of us (L.R.), and the complementary taxonomy by the other (P.S.G.).

[1] Part I was published in Jour. Arnold Arb. **47**: 222–247. 1966.

ly it does not appear to differ significantly from the diploid. In *L. alpigena* L., Poucques (1949, pp. 129 & 186) has recorded $n = 9$ and $2n = 18$, both of which numbers were confirmed by counts on a plant in the Arnold Arboretum (AA 91–60) which, unfortunately, died before an authenticating herbarium specimen was collected. However, in this species, the tetraploid number, $2n = 36$, has been found in two plants of f. *nana* (Carr.) Zabel (see below). In *L. maximowiczii* (Rupr.) Maxim. var. *sachalinensis* Fr. Schmidt we can now document a tetraploid ($n = 18$ and $2n = 36$), in contrast to the diploid number of $2n = 18$ recorded for the species by Janaki Ammal & Saunders (1952, p. 540). The plant on which their count was based does not appear to have been documented and it is now impossible to know which variety may have been involved, or to confirm its identity. Lastly, in our first paper we recorded a plant of *L. modesta* Rehd. var. *modesta* as diploid ($n = 9$ and $2n = 18$) and of var. *lushanensis* Rehd. as tetraploid ($n = 18$ and $2n = 36$), both plants having been raised from seed sent from the Lushan Botanic Gardens in China. Here, however, there is need for taxonomic reassessment, as we have pointed out (Rüdenberg & Green, 1966, p. 225). Available herbarium material has proved inadequate to enable one to come to a sound conclusion, but it may well prove that two species are involved where diagnostic distinctions need careful delineation.

It is, perhaps, worth drawing attention to the fact that in the whole of both subsections Tataricae and Ochranthae, including many cultivars and hybrids, but with one exception, no polyploid plants have been observed. The exception is *Lonicera floribunda* Boiss. & Buhse (AA 341–44) which is tetraploid. Within and between these subsections hybridization takes place readily, yet meiosis in most of these diploid hybrids is, with the exception of some plants with bridges, perfectly normal. A few of the plants studied at the Arnold Arboretum form bridges at anaphase I, especially *L.* × *bella*; meiosis was, therefore, checked the next year to determine its constancy and whether or not the frequency of these bridges could be correlated with the seasonal variation in climate. It was found that the number of cells showing bridges was not the same for the two years. It was smaller after the more normal spring, in contrast to one with especially cold nights and periods of drought.

## LITERATURE CITED

Janaki Ammal, E. K., & B. Saunders. 1952. Chromosome numbers in species of *Lonicera*. Kew Bull. **1952**: 539–541.

Löve, A. 1968. IOPB Chromosome number report XIX. Taxon **17**: 573–577.

Löve, A., & D. Löve. 1966. Cytotaxonomy of the alpine vascular plants of Mount Washington. Univ. Colorado Studies, Ser. Biol. **24**: 1–74.

Poucques. M.-L. de. 1949. Recherches caryologiques sur les Rubiales. Revue Gén. Bot. **56**: 5–27, 74–138, 172–188. [*Lonicera* pp. 84–95, 129, 186.]

Rehder, A. 1903. Synopsis of the genus *Lonicera*. Ann. Rep. Missouri Bot. Gard. **14**: 27–232.